Endothermy and chorusing behaviour in the African platypleurine cicada *Pycna semiclara* (Germar, 1834) (Hemiptera: Cicadidae)

Martin H. Villet, Allen F. Sanborn, and Polly K. Phillips

Abstract: Cicadas use acoustic signals to find mates and therefore offer a phylogenetically independent opportunity to test the generality of ideas about acoustic communication that were developed from studies of other animals. *Pycna semiclara* (Germar, 1834) (Hemiptera: Cicadidae) is a forest-dwelling platypleurine cicada that uses its calling song to form choruses and attract mates. Additionally, *P. semiclara* produces an encounter call that is involved in courtship and also in spacing males within choruses. Males generally call from exposed trunks and branches within the understory but clear of the undergrowth and fight with other males that call within about 50 cm of them. Choruses sing sporadically throughout the day but focus most of their calling activity into half-hour bouts at dawn and dusk. Body size and ambient temperature had no significant effect on spectral or temporal characteristics of the calling song. Body temperature measurements indicate that *P. semiclara* thermoregulates endothermically, with a body temperature of more than 22 °C above ambient temperature being measured during calling activity at dusk. Such endothermy provides an advantage to the cicadas by allowing them to call during crepuscular hours when atmospheric conditions are most optimal for acoustic communication and predation risks are minimal. Coincidentally, endogenously regulating body temperature allows the temporal characteristics of the call to be unaffected by ambient temperature changes.

Résumé : Les cigales utilisent des signaux acoustiques pour se trouver des partenaires; elles représentent donc un syst-phylogénétiquement indépendant pour vérifier la généralisation des idées développées au sujet de la communication acoustique dans des études sur d'autres animaux. *Pycna semiclara* (Germar, 1834) (Hemiptera : Cicadidae) est une cigale de la sous-famille des platypleurinés qui habite la forêt et qui utilise son chant d'appel pour former des choeurs et pour attirer des partenaires. De plus, *P. semiclara* produit un appel de rencontre qui sert dans le comportement de cour et aussi pour l'espacement des mâles dans un choeur. Les mâles émettent généralement leurs appels sur des troncs et des branches exposés sous le couvert des arbres, mais au-dessus du sous-bois, et ils combattent les autres mâles qui font des appels à moins d'environ 50 cm. Les choeurs chantent de façon sporadique pendant la journée, mais ils concentrent la majorité de leurs appels dans des épisodes d'une demi-heure à l'aube et au crépuscule. La taille du corps et la température ambiante n'ont aucun effet significatif sur les caractéristiques spectrales ou temporelles du chant d'appel. Des mesures de température du corps révèlent que *P. semiclara* fait une thermorégulation endotherme et que sa température peut atteindre jusqu'à 22 °C au-dessus de la température ambiante lors des activités d'appel au crépuscule. Une telle endothermie procure un avantage aux cigales en leur permettant de faire leurs appels durant les heures du crépuscule lorsque les conditions sont optimales pour la communication acoustique et les risques de prédation minimaux. En même temps, la régulation endogène de la température du corps assure que les caractéristiques temporelles de l'appel ne sont pas affectées par les changements de température ambiante.

[Traduit par la Rédaction]

Introduction

Cicadas, which Myers (1929) referred to as "the insect singers", use acoustic signals to find mates and therefore offer a phylogenetically independent opportunity to test the generality of ideas about acoustic communication that were developed from studies of other animals. Calling activity in birds, frogs, and orthopterans is well understood relative to what is known about cicadas. Even so, recent studies have examined the timing of chorusing (Crawford and Dadone 1979; Young 1981; Sanborn et al. 1995*a*; Sanborn 1997; Ewart 2001), the significance of call site (Doolan and MacNally 1981; Sanborn and Phillips 1995), interactions between individuals within choruses (Doolan 1981; Cocroft and Pogue 1997; Marshall and Cooley 2000; Cooley 2001), chorus dynamics (Lloyd and Karban 1983; Anonymous 1991; Williams and Smith 1991; Sueur and Aubin 2002), and responses to predators (Nagamine and Ito 1980; Gwynne 1987; Cooley 2001). Apart from the sheer numbers in some cicada choruses, which can exceed thousands in periodical cicadas, their behaviour has generally been reminis-

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cent of other animals that use acoustic signals. However, unlike these animals, some cicadas are facultative endotherms (Sanborn et al. 1995*a*, 1995*b*; Sanborn 2000), which has implications for their signalling behaviour.

Body temperature (T_b) has been shown to regulate acoustic behaviour, including altering when cicadas can call and the activity of the sound production system (see summary in Sanborn 2002). Reports of the effect of ambient temperature (T_a) on call parameters in cicadas have been contradictory, with the call parameters of some species exhibiting a relationship to T_a, while the call parameters of other species are independent of T_a (Popov 1975; Gogala et al. 1996; Popov et al. 1997; Sanborn and Maté 2000; Quartau et al. 2000).

This study presents data on the calling behaviour and physiology of *Pycna semiclara* (Germar, 1834) (Hemiptera: Cicadidae), a platypleurine cicada from southern Africa. It is moderately large, weighing about 1 g, and its wings are patterned with green, brown, and translucent patches and covered with silvery hairs. The calls of this species, and their functions, were described by Villet (1987, 1988, 1992).

Materials and methods

Pycna semiclara is distributed through the eastern region of South Africa from the Zoutpansberg in Northern Province, through Mpumalanga and the coastal and montane areas of KwaZulu-Natal, to the forested areas of Eastern Cape. The calling behaviour of *P. semiclara* was observed in the field at Mtunzini on the north coast of KwaZulu-Natal (28°58′S, 31°46′E) between October 1984 and January 1985 and in the Eastern Cape near Bedford (32°40′S, 26°01′E) and around Grahamstown (33°19′S, 26°32′E) in December 2001.

Calling males were located in the field by tracing calls to their source. The characteristics of the call sites were quantified and notes were made on the behaviour of individual males and on interactions within and between choruses, when such forms of interaction were found. The amount of time that individuals and choruses spent calling and the distance between nearest calling neighbours were measured. The calling activity of six neighbouring choruses was recorded every 10 min for 3 days. This sampling period was chosen because an individual's average calling duration was about 8 min (see Results). This would prevent an overestimation of chorus activity through sampling a short chorus at its start and end. The choruses were formed in riverine forest along a bend in a stream running through agricultural lands and were 50–130 m apart.

Sound recordings of calls were made at Mtunzini on a Nagra III tape recorder at a recording speed of 38.1 $\mathrm{cm \cdot s^{-1}}$ using a Beyer M69N dynamic microphone and a 3-m lead. The T_a at about 1 m above ground in the shade was recorded with a Physitemp BAT-12 digital thermometer fitted with a PT-6 probe when each call was recorded. Many specimens were then caught and the base to apex length of the forewing measured with vernier calipers. Call parameters were quantified using sonograms and power spectra made on a Kay 7029A sound spectrum analyzer. The time axis was calibrated with a Kay 6077A time marker.

The T_b of singing males and the T_a of their surroundings were measured in the Eastern Cape using a Physitemp BAT-12 digital thermometer and a Physitemp MT-29/1 hypodermic microprobe sensitive to ±0.1 °C with a time constant of $0.015 \cdot \mathrm{s^{-1}}$. Calling animals were captured with a net or by hand and their T_b measured by inserting the hypodermic probe midway into the dorsal mesothorax within 5 s of capture. The T_a was measured at a height of approximately 1 m in the shade.

Metabolic rates were estimated from heating and cooling curves produced by tethered animals. A copper–constantan thermocouple probe was implanted into the dorsal mesothorax of the cicadas to measure changes to T_b as they endogenously warmed when disturbed and as they cooled when placed in a container after their T_b had reached a plateau. The T_b was measured every 15 s as they heated (over 5 min) and cooled (over 15 min) with the BAT-12 digital thermometer. Heating and cooling curves constructed from these data were used to estimate the energetic expenditure involved in heating using the techniques described in Heath and Adams (1969) and Sanborn et al. (1995*a*). Captive specimens were weighed on a triple-beam balance (OHaus Scale Corporation, Florham Park, N.J.) sensitive to ±5 mg. All statistics are reported as mean ± SD.

Results

Call sites

Pycna semiclara is characteristically found in forests and plantations where undergrowth rarely grows taller than 1.2 m and the trees are at least 4 m in height. The species also occurs in large stands of oak (*Quercus* sp.), pines (*Pinus* spp.), gums (*Eucalyptus* spp.), and cottonwood (*Populus* sp.) with closed canopies. A few specimens were found in dense riverine bush and Eastern Cape valley bushveld, but this was very unusual.

Specimens at Mtunzini perched in the forest understorey above the level of the undergrowth (Fig. 1A) on the trunk and thicker branches (Fig. 1B) of a wide variety of trees (Table 1). Over 92% of the sites were within about 10° of vertical. In commercial pine plantations in the Sabie area (25°S, 30°E), where the lower branches had been lopped to a height of over 10 m, *P. semiclara* was found 7 m up the trunks, while in the Laingsnek Pass (27°29′S, 29°53′E), specimens were seen calling from as high as 11 m on the trunks of cottonwood trees, each over 15 m tall. At both of these latter localities, there was virtually no undergrowth, and some individuals were calling within a metre of the ground. All call sites were in shade, but generally exposed, with a good view of the surroundings. In 11 years of observations, only two specimens were seen landing in a sunny patch, and they immediately walked to shade before starting to sing.

Chorus behaviour

When a male of *P. semiclara* began to sing, those conspecifics nearby joined in or phonoresponded, and a chorus often formed. Spatially distinct choruses were as close as 50 m apart and contained 5–10 singing males at their peak. Call sites within the choruses at Mtunzini were usually 3–8 m apart (Fig. 2), with a mean of 5.13 m (n = 61). A lone

Fig. 1. Characteristics of call site perches used by *Pycna semiclara* in the coastal forest at Mtunzini. (A) Height of call sites above ground. (B) Diameters of call site perches.

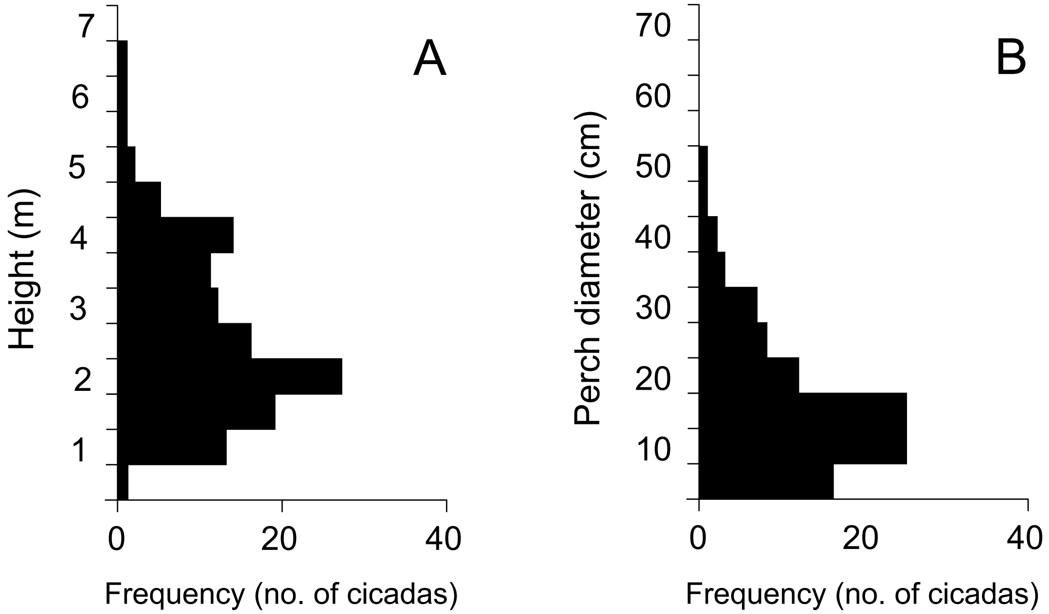


Table 1. Tree species on which adult *Pycna semiclara* were found perching or feeding (asterisk) at Mtunzini, South Africa.

Ficus natalensis Hochst. (Moraceae)
Ocotea bullata (Burch.) Baill. (Lauraceae)*
Albizia adianthifolia (Schumach.) (Leguminosae)*
Dalbergia armata E. Mey. (Leguminosae)
Erithrina lysistemon Hutch. (Leguminosae)
Milletia grandis (E. Mey.) Skeels (Leguminosae)
Antidesma venosum E. Mey. ex Tul. (Euphorbiaceae)
Macaranga capensis (Baill.) Benth. (Euphorbiaceae)
Hibiscus tilliaceus L. (Malvaceae)*
Barringtonia racemosa (L) Spreng. (Lecythidaceae)*
Syzygium cordatum Hochst. (Myrtaceae)*
Cussonia sphaerocephala Strey (Araliaceae)
Mimusops caffra E. Mey. ex A.DC. (Sapotaceae)
Euclea natalensis A. DC. (Ebenaceae)*
Olea woodiana Knobl. (Oleaceae)*
Strychnos spinosa Lam. (Loganaceae)
Voacanga thouarsii Roem., and Schult. (Apocynaceae)*

male was observed in the same tree for 4 days, walking or flying a metre or so each day. Males were generally sedentary but showed no fidelity to particular call sites.

Choruses were frequently heard at dawn, and often at dusk, each lasting for about half an hour, and there were sporadic bursts of chorusing throughout the day. The dawn chorus is obvious in Fig. 3, but windy conditions late in the day prevented the formation of evening choruses during this sampling period. In early summer the dawn chorus began at about 0430, moving to about 0400 as the days lengthened. The choruses started while it was still dark and stopped after sunrise; evening choruses ended just after dark. During the dawn chorus, individual males sang for about 25 ± 2.4 min (21–28 min, $n = 15$).

During the day, each male called for 7.9 ± 2.55 min on average (2–14 min, $n = 27$), but because of overlaps between individuals, choruses lasted up to half an hour. (Some choruses in Fig. 3 appear to last longer; this is an artifact of the 10-min sampling precision, which did not show briefer breaks in activity.) Neighbouring choruses often synchronized their calling activity during the day (Fig. 3).

Spacing behaviour

Males of *P. semiclara* flew to and landed on loudspeakers playing recordings of the conspecific calling song (described in Villet 1987). If a silent male came within 50 cm of a calling conspecific (i.e., the hatched area in Fig. 2), the caller would change its song to the encounter call (described in Villet 1987). The newcomer would either flee or start singing the encounter call too. The “resident” male approached, clawed at the newcomer’s head with its forelegs, and flicked its wings if it was alongside the newcomer, which sometimes dislodged the newcomer. The newcomer retaliated, until one or the other specimen fled, usually on foot and pursued by the other. Once the specimens were over 50 cm apart, calling song production was resumed.

The same pattern of interaction occurred when two males approached one another by walking on the tree. When the callers were once again over 50 cm apart, they returned to normal calling song. Twice, a pair of males continued to produce encounter calls even though they had moved out of sight of one another but were still within 50 cm of one another. Only when one male fell silent did the other resume the normal calling song. This implies that these males could hear others even while singing their encounter song.

On three occasions, specimens of the butterfly *Sallaya natalensis* (Boisduval) (Lepidoptera, Nymphalidae) approached calling males of *P. semiclara* by walking along the trunk. In each case the male changed to its encounter song but did

Fig. 2. Distances between neighbouring calling males in choruses of *P. semiclara* at Mtunzini. Solid bars denote males producing calling song; hatched bars denote males producing encounter calls.

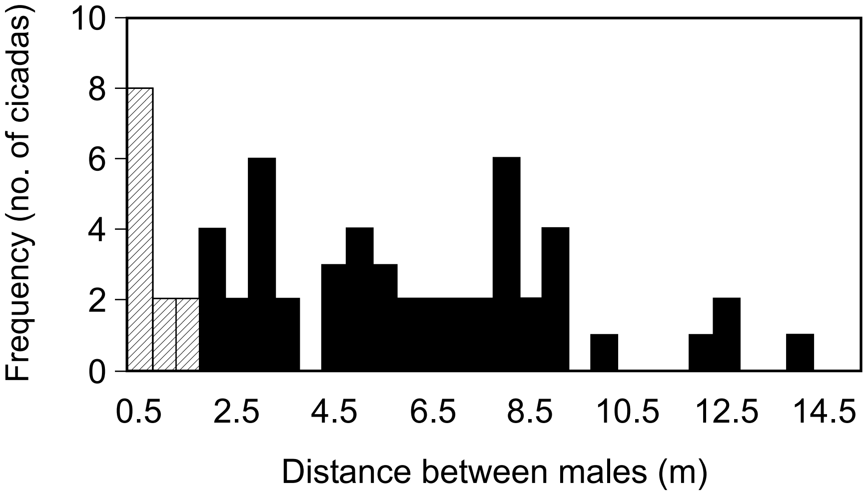
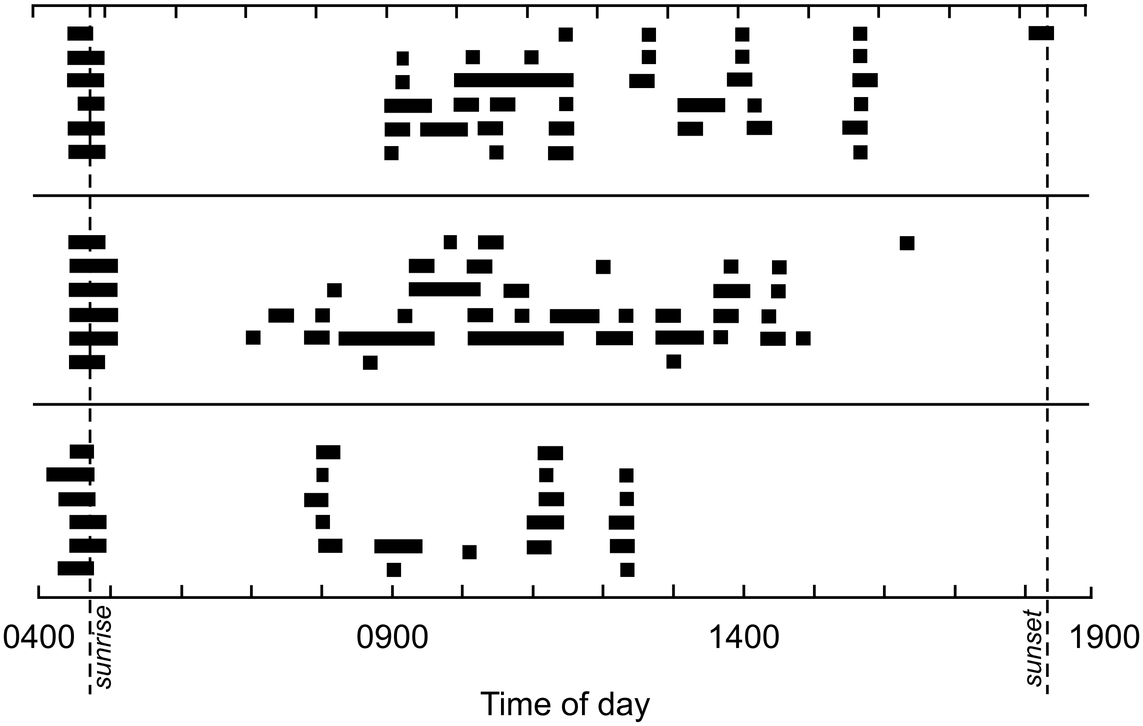


Fig. 3. Chorusing activity in six choruses of *P. semiclara* over 3 consecutive days in coastal forest at Mtunzini. The choruses are presented in the same order on each day and are arranged in order of proximity to one another. The vertical lines represent the time of sunrise and sunset.



not move forward and flew off when the butterfly came within 15 cm of it.

Encounter calls were also produced as an overture to the calling song.

Courtship behaviour

When females landed near a calling male, the male responded to the newcomer as described above, changing its call, clawing, and wing flicking. Receptive females did not move or retaliate to the male's clawing and wing flicking, while unreceptive females did so briefly before flying off. If the female did not move, the male fell silent and copulation ensued.

Temperature and call parameters

The calling song of *P. semiclara* is a loud (106 dB), monotonous note that is not subdivided into echemes (Villet 1987, 1988). It is composed of harmonics of an almost pure-tone 400-Hz fundamental. A total of 54 calls were analyzed (Table 2). Their peak frequency (mean = 4.8 kHz) and pulse repetition rate (mean = 780 Hz) were not related to T_a (Spearman's r_S = 0.17 and 0.08, respectively, both not sig-

Table 2. Correlations of song parameters of *P. semiclara* with ambient temperature and body size.

		Temperature		Wing length	
Parameter	n	r_S	p	r_S	p
Emphasized frequency	57	0.1326	0.320	0.033	0.666
Pulse repetition rate	57	0.0646	0.320	0.397	0.094

nificantly different from 0.00), while the highest frequency was weakly related to temperature (Spearman's $r_S = 0.39$, $p < 0.05$).

Thermoregulation

The T_b of calling males ranged from 35.3 to 40.3 °C. There was no statistical difference (Student's t test, t = 0.2003, df = 7, p = 0.5765) between T_b measured in diurnally calling males (37.85 ± 1.58 °C, n = 6) and T_b in those calling in the evening or in the laboratory without access to solar radiation (37.6 ± 2.13 °C, n = 4). The T_b's measured in animals without access to solar radiation were 15.63 ± 5.42 °C (n = 2) above T_a. The T_b's of animals measured during the evening chorus were 17.5 and 22.3 °C above ambient.

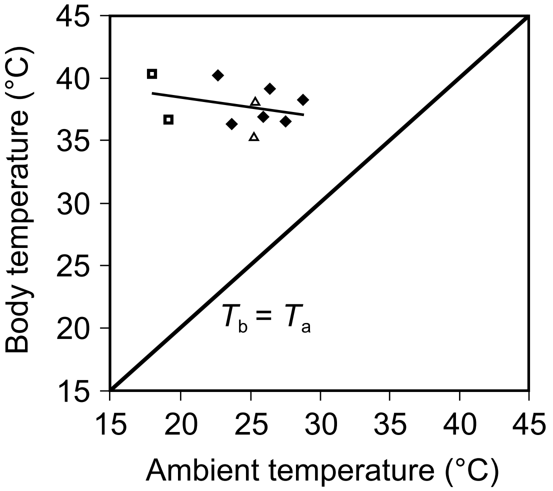
The slope of the regression of T_b as a function of T_a is an indication of T_b regulation. Thermoregulation is occurring if the slope of the regression is significantly different from 1 (May and Casey 1983; May 1985). Figure 4 illustrates the distribution of T_b as a function of T_a. The slope of the regression is significantly different from 1 (t = –6.988, df = 8, p < 0.0001) and not significantly different from 0 (t = 0.9273, df = 8, p = 0.1904), suggesting that *P. semiclara* thermoregulates.

Specimens of *P. semiclara* cool at a rate of 0.154 ± 0.027 $°C \cdot min^{-1} \cdot °C\ gradient^{-1}$ (n = 5). The rate at which cicadas cool follows Newton's law of cooling, suggesting no regulation of heat loss by the animals. Mean mass of the animals used to generate the cooling curves was 0.978 ± 0.153 g (n = 5). Heat production occurred without visible wing movements or vibrations from the flight muscles, but telescoping movements of the abdomen did occur. Maximal oxygen consumption was calculated as 0.3623 mL $O_2 \cdot min^{-1}$ in the one male that would endothermically warm while attached to a probe. This is sufficient to generate a temperature gradient of 39.71 °C in an average *P. semiclara*. To maintain the maximum 22.3 °C gradient observed in the field, a *P. semiclara* would have to use only 0.2449 mL $O_2 \cdot min^{-1}$.

Discussion

Doolan and MacNally (1981) showed that call site selection was important in determining the reproductive success of *Cystosoma saundersii* (Westwood) through improving signal transmission, and this is probably also the case in *P. semiclara*. By selecting perches between the undergrowth and the canopy layers, sound attenuation will be reduced due to scattering and absorption by the vegetation (Aylor 1972; Linskens et al. 1976; Wiley and Richards 1978, 1982; Richards and Wiley 1980). This should optimize the detectability and locatability of the signaller to legitimate (and illegitimate) receivers. Other characteristics of the perch sites appear to be related to avoiding predation. The good vista from these perches would enable the cicadas to see vertebrate predators approaching before they become a threat. Specimens tend to fall silent when they see humans several metres away and usually fly off when one approaches within 2 or 3 m of them. That three specimens were seen fleeing from butterflies emphasizes their skittishness. Perching on thicker trunks and branches reduces the visual conspicuousness of these large-bodied bugs, as does their umbrophilous perch selection and their camouflaging wing pigmentation, so that predators are at a distinct disadvantage in locating them even though their calls are loud and conspicuous. Predation can be a major force shaping acoustic signalling systems (Zuk and Kolluru 1998), and the circumstantial evidence suggests that it is significant in *P. semiclara*. There was no evidence that call sites were associated with resources that might be useful in reproduction, and males abandoned call sites readily if threatened. However, they often stayed in the same tree for several days, as do males of *C. saundersii* (Doolan and MacNally 1981). In *P. semiclara*, this behaviour may be interpreted as an unwillingness to give away their position to active predators by moving or to expose themselves to sit-and-wait predators like spiders. There is ample scope for testing this hypothesis.

Fig. 4. Relationship between ambient temperature (T_a) and cicada body temperature (T_b) during calling in *P. semiclara* ($T_b = 41.467 - 0.15288T_a$, $r^2 = 0.097$). The slope of the regression is significantly different from 1 (t = –6.988, df = 8, p < 0.0001) and not significantly different from 0 (t = 0.9273, df = 8, p = 0.1904), suggesting thermoregulation. Diamonds, diurnal calling animals; squares, animals calling in the evening chorus; triangles, animals calling in the laboratory; open symbols, situations with negligible radiant heat sources such as sunlight.



Spatial aggregation to form choruses of *Magicicada* spp. appears to be related initially to sites where emergence densities were high but then became dynamic with respect to location during the total adult activity period (Williams and Smith 1991). The value of spatial aggregation in this species is generally agreed to be predator saturation. The chorus centres of *P. semiclara* are also spatially dynamic but form when males phonorespond by flying towards calling individuals (Villet 1992). These choruses are not dense enough, and individuals are too shy, for predator saturation to occur. Comparable findings have been made regarding spatial aggregation in *C. saundersii* (Doolan and MacNally 1981).

The formation of a chorus may be expected to lead to a higher degree of competition among males for mates, and males of *P. semiclara* certainly show aggressive spacing behaviour. Spacing behaviour occurs passively in choruses of *C. saundersii* and has been suggested to decrease acoustic interference and sexual (specifically acoustic) parasitism between males (Doolan 1981); it probably also has these competitive functions in *P. semiclara*. Territoriality may arise if males can exclude each other from resources useful in the reproductive process. Because cicada chorus sites are spatially dynamic, they are apparently not specifically associated with resources that might be valuable to reproduction. However, chorus formation increases the range that an acoustic signal travels, and in *C. saundersii*, males that join choruses achieve more matings per capita than males calling alone (Doolan and MacNally 1981), so that sexual competition is actually alleviated. This may also explain the domino-like-effect triggering of nearby choruses (Fig. 3) as a collaborative rather than a competitive or parasitic behaviour. In addition, adequate spacing helps to make individuals more locatable to females and to prevent neighbouring conspecifics from attracting predators to one. Competition is therefore only one of several interacting explanations for cicada choruses.

It is necessary to initiate a female courtship response in *C. saundersii* (Doolan 1981). In this context, the role of the encounter call in courtship in *P. semiclara* is ambiguous, and perhaps adaptively so, since it may serve both to repel neighbouring males and to promote receptiveness to mating in females. Since male–male interactions are the more common context for encounter calls, it may not pay males to investigate others making encounter calls on the chance of discovering a receptive female. Specifically, the risk of exposure to predators while moving to investigate may outweigh the occasional rewards of locating a potential mate. The ambiguity of the encounter call implies that it is a deceptive signal to competitors in certain contexts (i.e., when it is provoked by a female), a hypothesis that should be addressed empirically.

The wing-flicking behaviour seen in *P. semiclara* is performed only by males and also serves an ambiguous role, since it occurs in courtship and male–male agression. Erratic wing flicking in both sexes of *Okanagana* spp. has been attributed to parasite deterence and to courtship (Cooley 2001), while a variety of cicadas show wing flicking by females that is a ritualized part of courtship (e.g., Dugdale and Fleming 1969; Doolan 1981; Doolan and Young 1989; Cooley and Marshall 2001). Clearly, the same signal can serve more than one role, sometimes even within one species.

Pycna semiclara uses endogenous heat to regulate T_b in a manner similar to that of some other cicada species (Sanborn et al. 1995*a*, 1995*b*; Sanborn 2000). They call from perches that are generally in the forest understory, where they are shaded and T_b would approximate T_a if not for the endogenous heat production. We never observed *P. semiclara* basking in sunlight on the large branches or trunks that they used as perches. This contrasts with the facultative endothermy described in New World cicadas where solar radiation is used to regulate T_b when it is available (Sanborn et al. 1995*a*, 1995*b*; Sanborn 2000). *Pycna semiclara* appears to regulate T_b exclusively with endogenous heat. This suggests that there is strong reason to stay out of the sun, which might be interpreted as pressure to avoid becoming visible to predators.

Pycna semiclara is able to elevate T_b without flight or visible wing movements, as is also seen in the endothermic cicada *Tibicen winnemanna* (Davis) (Sanborn 2000). In contrast, *Fidicina mannifera* (Fabricius) produces small wing movements while endothermically elevating T_b (Bartholomew and Barnhardt 1984), while *Proarna bergi* (Distant) and *Proarna insignis* Distant produce shiver-like movements of the wings to generate heat (Sanborn et al. 1995*b*). No vibrations were felt in the temperature probe in *P. semiclara*, so heat generation might have been through a mechanism similar to the tetanic contractions reported in bees (Esch and Goller 1991). Circumstantial support for this mechanism is that it was difficult to provoke tethered specimens of cicadas to fly while endogenously warming during our thermal adaptation experiments.

The rate at which *P. semiclara* cool is partially related to their size. However, when compared with other cicadas, *P. semiclara* cool more slowly than larger endothermic species (Sanborn et al. 1995*a*). This may be related to the general shape of *P. semiclara*. *Pycna semiclara* has a short and stocky appearance, which would mean that it has a lower surface to volume ratio than a longer, thinner cicada. The decrease in the surface to volume ratio would translate to a decrease in the observed cooling rate. It is advantageous for *P. semiclara* to have a lower cooling rate, since *P. semiclara* appear not to use solar radiation and are completely dependent on endogenous heat for thermoregulation.

The endothermy exhibited by *P. semiclara* provides many of the same benefits that have been described in other cicada species (Sanborn et al. 1995*a*, 1995*b*; Sanborn 2000). *Pycna semiclara* were not inhibited from calling until T_a dropped to 17.8 °C with a relatively strong wind. Endothermy permits crepuscular calling, when sound travels farther (Henwood and Fabrick 1979; Wiley and Richards 1978; Larom et al. 1997) and predation risk is decreased due to the decrease in avian foraging efficiency with decreasing light intensities (Kacelnik 1979; Doolan and MacNally 1981; Zuk and Kolluru 1998). Crepuscular calling has been reported in several cicadas (e.g., Crawford and Dadone 1979; Young 1981; Ewart 2001). As in several Australian cicadas (Ewart 2001), choruses of *P. semiclara* track sunrise and sunset by adjusting their onset over the season. Crawford and Dadone (1979) showed that chorus onset in *Tibicen dealbatus* (Davis) was best correlated with light intensity and secondarily with changes in barometric pressure, but there is no direct evidence of the physiological mechanism governing the onset of crepuscular chorusing.

Even though *P. semiclara* uses endogenous heat to thermoregulate, reproductive behaviour can still be altered by T_a. Many authors (summarized in Sanborn 1998) have noted that calling behaviour is inhibited by low T_a. A low T_a or particularly a low T_a combined with convective heat loss is sufficient to inhibit calling in *P. semiclara*. The changes in *P. semiclara* acoustic output are related to changes in T_b as the animals warm. We noted that a specimen in the laboratory initially produced an encounter call at a T_b of 30.9 °C but produced a full calling song at a T_b of 35.3 °C. This is similar to the changes in acoustic behaviour seen in the endothermic *T. winnemanna* (Sanborn 1997).

One would not expect a relationship between call frequency and T_a. The frequency of cicada calls is dependent on the physics of the sound production system (Pringle 1954; Bennet-Clark and Young 1992). However, the temporal patterns of the call can be altered by the temperature effects on components of the sound production system. Action potential frequency in timbal nerves (Wakabayashi and Hagiwara 1953; Wakabayashi and Ikeda 1961), timbal muscle contraction kinetics (Aidley and White 1969; Josephson 1981; Josephson and Young 1979, 1985; Young and Josephson 1983; Sanborn 2001), and T_b (Josephson and Young 1979; Sanborn 1997) have all been shown to alter the temporal components of cicada calls. Endothermic thermoregulation in *P. semiclara* appears to eliminate any effect that T_a has on the temporal parameters of their call. This is important to the males in that changes in T_a will not alter the temporal pattern of their reproductive signal or affect their attractiveness to females (Villet 1995).

The behaviour of the butterfly *S. natalensis* to calling *P. semiclara* is reminiscent of that observed in some neuropterans (Lewis 1891; van Noort 1995). The giant lacewing *Ithalochrysa neurodes* (Rambur) was observed feeding from a puncture made in the stem by *Platypleura capensis* (Linnaeus) (van Noort 1995) and has also been found attending *Platypleura plumosa* (Germar) and *Capcicada decora* (Germar) (M.H. Villet, personal observation). *Sallaya natalensis* might be using *P. semiclara* in a similar manner to gain access to sap, and it is not clear if it is the call that attracts them.

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References

Aidley, D.J., and White, D.C.S. 1969. Mechanical properties of glycerinated fibers from the tymbal muscles of a Brazilian cicada. J. Physiol. **205**: 179–192.

Anonymous. 1991. Periodical cicadas may form communal choruses. Am. Entomol. **37**: 227.

Aylor, D. 1972. Noise reduction by vegetation and ground. J. Acoust. Soc. Am. **51**: 197–205.

Bennet-Clark, H.C., and Young, D. 1992. A model of the mechanism of sound production in cicadas. J. Exp. Biol. **173**: 123–153.

Cocroft, R.B., and Pogue, M. 1997. Social behavior and communication in the Neotropical cicada *Fidicina mannifera* (Fabricius) (Homoptera: Cicadidae). J. Kans. Entomol. Soc. **69**: 85–97.

Cooley, J.R. 2001. Long-range acoustic signals, phonotaxis, and risk in the sexual pair-forming behaviours of *Okanagana canadensis* and *O. rimosa* (Hemiptera: Cicadidae). Ann. Entomol. Soc. Am. **94**: 755–760.

Cooley, J.R., and Marshall, D.C. 2001. Sexual signalling in periodical cicadas, *Magicicada* spp. Behaviour, **138**: 827–855.

Crawford, C.S., and Dadone, M.M. 1979. Onset of evening chorus in *Tibicen marginalis* (Homoptera: Cicadidae). Environ. Entomol. **8**: 1157–1160.

Doolan, J.M. 1981. Male spacing and the influence of female courtship behavior in the bladder cicada, *Cystosoma saundersii* Westwood. Behav. Ecol. Sociobiol. **9**: 269–276.

Doolan, J.M., and MacNally, R.C. 1981. Spatial dynamics and breeding ecology in the cicada, *Cystosoma saundersii*: the interaction between distributions of resources and interspecific behavior. J. Anim. Ecol. **50**: 925–940.

Doolan, J.M., and Young, D. 1989. Relative importance of song parameters during flight phonotaxis and courtship in the bladder cicada *Cystosoma saundersii*. J. Exp. Biol. **141**: 113–131.

Dugdale, J.S., and Fleming, C.A. 1969. Two New Zealand cicadas collected on Cook’s Endeavour voyage, with a description of a new genus. N.Z. J. Sci. **12**: 929–957.

Esch, H., and Goller, F. 1991. Neural control of fibrillar muscles in bees during shivering and flight. J. Exp. Biol. **159**: 419–431.

Ewart, A. 2001. Dusk chorusing behaviour in cicadas (Homoptera: Cicadidae) and a mole cricket, Brisbane, Queensland. Mem. Queensl. Mus. **46**: 499–510.

Gogala, M., Popov, A.V., and Ribaric, D. 1996. Bioacoustics of singing cicadas of the western Palaearctic: *Cicadetta tibialis* (Panzer) (Cicadoidea: Tibicinidae). Acta Entomol. Slov. **4**: 45–62.

Heath, J.E., and Adams, P.A. 1969. Temperature regulation and heat production in insects. *In* Experiments in physiology and biochemistry. Vol. 2. *Edited by* G.A. Kerkut. Academic Press, New York. pp. 275–293.

Henwood, K., and Fabrick, A. 1979. A quantitative analysis of the dawn chorus: temporal selection for communicatory optimization. Am. Nat. **114**: 260–274.

Josephson, R.K. 1981. Temperature and the mechanical performance of insect muscle. *In* Insect thermoregulation. *Edited by* B. Heinrich. John Wiley & Sons, New York. pp. 19–44.

Josephson, R.K., and Young, D. 1979. Body temperature and singing in the bladder cicada, *Cystosoma saundersii*. J. Exp. Biol. **80**: 69–81.

Josephson, R.K., and Young, D. 1985. A synchronous insect muscle with an operating frequency greater than 500 Hz. J. Exp. Biol. **118**: 185–208.

Kacelnik, A. 1979. The foraging efficiency of great tits (*Parus major* L.) in relation to light intensity. Anim. Behav. **27**: 237–241.

Larom, D., Garstang, M., Payne, K., Raspet, R., and Lindeque, M. 1997. The influence of surface atmospheric conditions on the range and area reached by animal vocalizations. J. Exp. Biol. **200**: 421–431.

Lewis, R.T. 1891. Nature notes from South Africa. Nature Notes, Selborne Society Magazine, **2**: 141–142.

Linskens, H.F., Martens, M., Hendriksen, H., Roestenberg-Sinnige, A., Brouwers, W., van der Staak, A., and Strik-Jansen, A. 1976. The acoustic climate of plant communities. Oecologia, **23**: 165–177.

Lloyd, M., and Karban, R. 1983. Chorusing centers of periodical cicadas. J. Kans. Entomol. Soc. **56**: 299–304.

Marshall, D.C., and Cooley, J.R. 2000. Reproductive character displacement and speciation in periodical cicadas, with description of a new species, 13-year *Magicicada neotredecim*. Evolution, **54**: 1313–1325.

May, M.L. 1985. Thermoregulation. *In* Comprehensive insect physiology, biochemistry, and pharmacology. Vol. 4. *Edited by* G.A. Kerkut and L.I. Gilbert. Pergamon Press, New York. pp. 507–552.

May, M.L., and Casey, T.M. 1983. Thermoregulation and heat exchange in euglossine bees. Physiol. Zool. **56**: 541–551.

Myers, J.G. 1929. Insect singers: a natural history of the cicadas. George Routledge and Sons, London, U.K.

Nagamine, M., and Ito, Y. 1980. ‘Predator-foolhardiness’ in an epidemic cicada population. Res. Popul. Ecol. (Kyoto), **22**: 89–92.

Popov, A.V. 1975. The structure of the tymbals and the characteristics of the sound signals in singing cicadas (Homoptera, Cicadidae) in the southern regions of the USSR. Entomol. Rev. Wash. **54**: 7–35.

Popov, A.V., Beganovic, A., and Gogala, M. 1997. Bioacoustics of singing cicadas of the western Palaearctic: *Tettigetta brullei* (Fieber 1876) (Cicadoidea: Tibicinidae). Acta Entomol. Slov. **5**: 89–101.

Pringle, J.W.S. 1954. A physiological analysis of cicada song. J. Exp. Biol. **31**: 525–560.

Quartau, J.A., Seabra, S., and Sanborn, A. 2000. Effect of ambient air temperature on some temporal parameters of the calling song of *Cicada orni* Linnaeus, 1758 (Hemiptera: Cicadidae) in Portugal. Acta Zool. Cracov. **43**: 193–198.

Richards, D.G., and Wiley, R.H. 1980. Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. Am. Nat. **115**: 381–399.

Sanborn, A.F. 1997. Body temperature and the acoustic behavior of the cicada *Tibicen winnemanna* (Homoptera: Cicadidae). J. Insect Behav. **10**: 257–264.

Sanborn, A.F. 1998. Thermal biology of cicadas (Homoptera: Cicadoidea). Trends Entomol. **1**: 89–104.

Sanborn, A.F. 2000. Comparative thermoregulation of sympatric endothermic and ectothermic cicadas (Homoptera: Cicadidae: *Tibicen winnemanna* and *Tibicen chloromerus*). J. Comp. Physiol. A Sens. Neural Behav. Physiol. **186**: 551–556.

Sanborn, A.F. 2001. Timbal muscle physiology in the endothermic cicada *Tibicen winnemanna* (Homoptera: Cicadidae). Comp. Biochem. Physiol. A, **130**: 9–19.

Sanborn, A.F. 2002. Cicada thermoregulation (Hemiptera, Cicadoidea). Denisia, **4**: 455–470.

Sanborn, A.F., and Maté, S. 2000. Thermoregulation and the effect of body temperature on call temporal parameters in the cicada *Diceroprocta olympusa* (Homoptera: Cicadidae). Comp. Biochem. Physiol. A, **125**: 141–148.

Sanborn, A.F., and Phillips, P.K. 1995. No acoustic benefit to subterranean calling in the cicada *Okanagana pallidula* Davis (Homoptera: Tibicinidae). Great Basin Nat. **55**: 374–376.

Sanborn, A.F., Heath, M.S., Heath, J.E., and Noriega, F.G. 1995*a*. Diurnal activity, temperature responses and endothermy in three South American cicadas (Homoptera: Cicadidae: *Dorisiana bonaerensis*, *Quesada gigas*, and *Fidicina mannifera*). J. Therm. Biol. **20**: 451–460.

Sanborn, A.F., Heath, J.E., Heath, M.S., and Noriega, F.G. 1995*b*. Thermoregulation by endogenous heat production in two South American grass dwelling cicadas (Homoptera: Cicadidae: *Proarna*). Fla. Entomol. **78**: 319–328.

Sueur, J., and Aubin, T. 2002. Acoustic communication in the Palaeactic red cicada, *Tibicina haematodes*: chorus organisation, calling-song structure, and signal recognition. Can. J. Zool. **80**: 126–136.

van Noort, S. 1995. An association of *Italochrysa neurodes* (Rambur) (Neuroptera: Chyrsopidae) with *Platypleura capensis* (Linnaeus) (Hemiptera: Cicadidae). Afr. Entomol. **3**: 92–94.

Villet, M.H. 1987. Sound pressure levels of some African cicadas (Homoptera: Cicadoidea). J. Entomol. Soc. South. Afr. **50**: 269–274.

Villet, M.H. 1988. Calling songs of some South African cicadas (Homoptera: Cicadidae). S. Afr. J. Zool. **23**: 71–77.

Villet, M.H. 1992. Responses of free-living cicadas (Homoptera: Cicadidae) to broadcasts of cicada songs. J. Entomol. Soc. South. Afr. **55**: 93–97.

Villet, M.H. 1995. Intraspecific variability in SMRS signals: some causes and implications in acoustic signalling systems. *In* Species and the recognition concept: theory and application. *Edited by* D.M. Lambert and H.G. Spencer. Johns Hopkins University Press, Baltimore, Md. pp. 422–439.

Wakabayashi, T., and Hagiwara, S. 1953. Mechanical and electrical events in the main sound muscle of cicada. Japan. J. Physiol. **3**: 249–253.

Wakabayashi, T., and Ikeda, K. 1961. Interrelation between action potential and miniture electrical oscillation in the tymbal muscle of the cicada. Japan. J. Physiol. **11**: 585–595.

Wiley, R.H., and Richards, D.G. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalization. Behav. Ecol. Sociobiol. **3**: 69–94.

Wiley, R.H., and Richards, D.G. 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection. *In* Acoustic communication in birds: production, perception, and design features of sound. Vol. 1. *Edited by* D.E. Kroodsma and E.H. Miller. Academic Press, New York. pp. 131–181.

Williams, K.S., and Smith, K.G. 1991. Dynamics of periodical cicada chorus centers (Homoptera: Cicadidae: *Magicicada*). J. Insect Behav. **4**: 275–291.

Young, A.M. 1981. Temporal selection for communicatory optimization: the dawn–dusk chorus as an adaptation in tropical cicadas. Am. Nat. **117**: 826–829.

Young, D., and Josephson, R.K. 1983. Pure-tone songs in cicadas with special reference to the genus *Magicicada*. J. Comp. Physiol. A Sens. Neural Behav. Physiol. **152**: 197–207.

Zuk, M., and Kolluru, G.R. 1998. Exploitation of sexual signals by predators and parasitoids. Q. Rev. Biol. **73**: 415–438.